Kerguelen Islands: a living laboratory to understand the benthic biodiversity of the Antarctic

by

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ABSTRACT. - The high proportion of brooding (50 to 70% depending on phyla) compared with broadcaster species among invertebrates living along the coast of the Southern Ocean has been traditionally interpreted as an adaptation to local environmental conditions. Currently, however, species with a planktotrophic developmental mode are ecologically dominant along coastal areas, in terms of abundance of individuals. The fact that Kerguelen Island is inhabited by such species and that the French base Port-aux-Français, with its equipped marine laboratory, made it possible to address questions as to why are there so many brooders in the coastal waters of the Southern Ocean and if the apparent ecological success of broadcasters related to their developmental mode. We argue that the present shallow Antarctic benthic invertebrate fauna is the result of two processes acting at different temporal scales. First, the high proportion of brooding species compared with coastal communities elsewhere corresponds to species-level selection occurring over geological and evolutionary times which explains the very high biodiversity observed in coastal waters. Second, the ecological dominance of broadcasters is the result of processes operating at ecological timescales that are associated with the advantage of having pelagic larvae under highly disturbed conditions (e.g., ice scouring).

RÉSUMÉ. - Les îles Kerguelen : un laboratoire vivant pour la compréhension de la biodiversité benthique en Antarctique.

La proportion élevée (50 à 70% selon les phylums) d'espèces incubantes comparée à celle des espèces dispersantes d'invertébrés vivant dans les eaux côtières de l'océan Austral a été traditionnellement interprétée comme une adaptation aux conditions environnementales locales. Cependant, de nos jours, les espèces à développement planctotrophique y sont écologiquement dominantes, en termes d'abondance. Le fait que les îles Kerguelen abritent de telles espèces et que la base de Port-aux-Français possède un véritable laboratoire marin a permis de développer des programmes pour répondre à des questions comme : pourquoi y-a-t-il tant d'espèces incubantes dans les eaux côtières de l'océan Austral ? Ou bien, le succès écologique apparent des espèces dispersantes est-il lié à leur mode de développement ? Nous soutenons que la faune actuelle d'invertébrés benthiques côtiers antarctiques est le résultat de deux processus agissant à des échelles temporelles différentes : (1) la proportion élevée d'espèces incubantes, comparée aux communautés côtières partout ailleurs, correspond à une sélection au niveau de l'espèce se produisant à des échelles de temps géologiques qui explique la biodiversité très élevée observée dans les eaux côtières, (2) la dominance écologique actuelle des espèces dispersantes est le résultat de processus fonctionnant à des échelles de temps écologiques qui sont associés à l'avantage de posséder des larves pélagiques dans des conditions fortement perturbées (p. ex., rabotage des fonds par les icebergs).

Key words. - Brooding invertebrates - Coastal communities - Southern Ocean - Biodiversity.

Since the seventies, benthic biodiversity was assessed in Kerguelen during the cruises of the *Marion Dufresne* and thanks to programs by R. Delépine and others focused on algae, P. Arnaud, A. Guille, J.-P. Féral on macrobenthos and by J.-C. Hureau and G. Duhamel on fishes. Pioneering efforts to study the Antarctic biodiversity in Terre Adélie were conducted by P. Arnaud and J.-C. Hureau in the early sixties and in 1987 by the first diving expedition by J.-P. Féral. Initial investigations of Antarctic marine biology started with macrobenthos and fishes. The use of scuba diving, limited exploration only until 30 m depth; the use of a remote operated vehicle (ROV) in 2000 permitted the study of biodiversity at 150 m depth. The *Astrolabe*, equipped with a ROV, verified previous observations.

Contrary to an accepted (continental-based) paradigm that biodiversity declines from the equator to the poles, marine biodiversity, at least coastally, is very high along the Antarctic continent and the sub-Antarctic islands. As the observed biodiversity at a time is the result of the histories of the species, of the climate and of the ocean basins, it is necessary to consider different time scales to understand the present biodiversity. To only compare contemporary conditions with the characteristics of the fauna and flora is quite risky. Hence, we propose to first consider exceptional biological properties of the Antarctic fauna, using model species.

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The Southern Ocean's coastal waters are remarkable because they are inhabited by a great majority of brooding invertebrate species

Marine invertebrates display a great variety of life-history traits and reproductive strategies. Each broad type of free and protected development is found in all the oceans, but comparisons of the principal reproductive modes between different geographic regions have shown that they are not equally distributed. Frequency of pelagic development (planktotrophic and lecithotrophic) decreases from the Equator to the Antarctic, where brood-protecting becomes dominant. The high proportion of brooding (50-70% depending on phyla) compared with broadcasting species among invertebrates living along the coast of the Southern Ocean has been traditionally interpreted as an adaptation to local environmental conditions. On the other hand, in the present days, species with a planktotrophic developmental mode are ecologically dominant along coastal areas of the Southern Ocean, in terms of abundance of individuals.

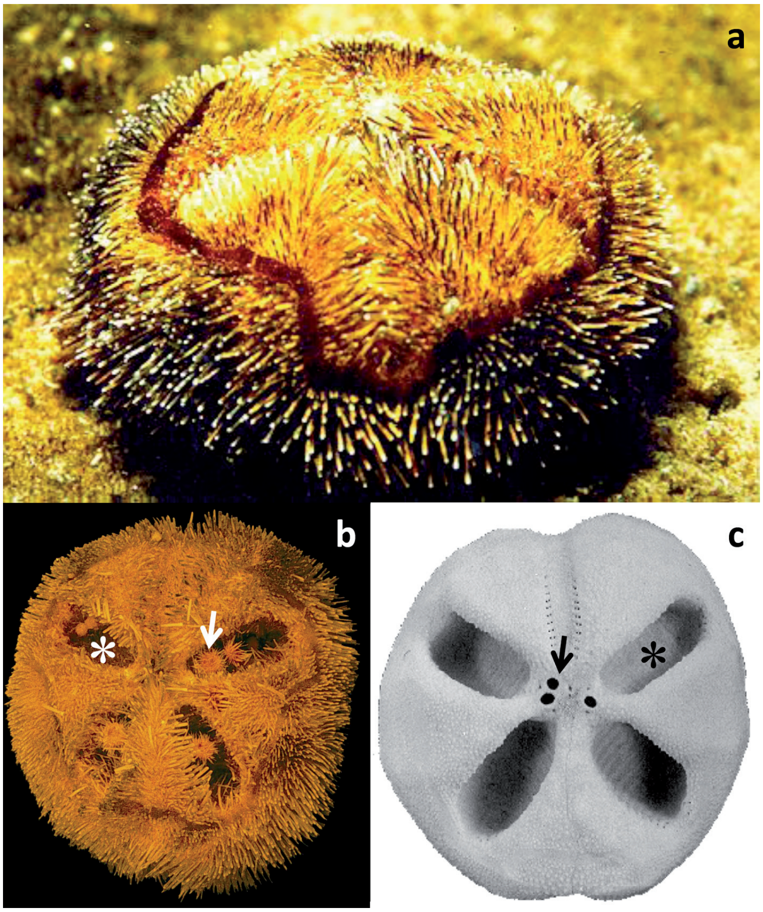

Figure 1. - *Abatus cordatus*. (a) natural aspect (b) female individual with removed spines over the brooding pouches (white star) showing the offspring (white arrow), (c) female test showing the four aboral brooding pouches (black star) and the three gonopores (black arrow). © photos by J.C. Duchêne (a), J.P. Féral (b) and P. Magniez (c).

Developing explanatory hypotheses

Numerous theories have been proposed to explain the richness of non-pelagic development in most marine invertebrates within the Southern Ocean. These theories can be grouped into three categories: larval survival (where selection acts on larvae), energy allocation, and dispersal. All of them consider the adaptive significance of brood-protecting as the key to the success of this strategy in the Antarctic. However, the adaptive significance of brooding and the evolutionary success of this strategy in the Antarctic must be considered as two separate issues.

Considering the problem from an evolutionary level, the consequences of different reproductive strategies on the genetic structure of species and on the long-term evolution of the clade were examined.

Sea urchins as a model class

In echinoids, the reduction of larval stage duration is associated with a decrease in gene flow and consequently of the geographical scale of genetic differentiation. Four patterns of larval development are generally recognized: planktotrophy, pelagic lecithotrophy, bottom dwelling and brood-protecting. Non-pelagic development is clearly the rule for Antarctic echinoids. The 79 nominal echinoid species known from Antarctic and Subantarctic areas belong to nine families (four being exclusively abyssal). Around 65% have non-pelagic development (all brooding) and 35% with pelagic development. Two families, the Schizasteridae (Spatangoida) and the Cidaridae (Cidaroida), consist almost entirely of brooding species. The developmental type of a few cidaroid species is still unknown. A third family, the Echinidae (Echinoida), consists of six species that have a planktotrophic larva. These three families are the typical echinoids in the Antarctic coastal and shallow waters. The Echinothuriidae and the three families of Holasteroida known from Antarctic waters, the Urechinidae, the Plexechinidae and the Pourtalesiidae are essentially deep-sea forms with a wide distribution in the ocean basins.

Where and how to study the diversification of echinoids?

To understand the impacts and the interest in brood protection, it was necessary to study the echinoids' life cycle and ecology. Because most life cycles are annual, and given the constraints of scuba diving in Terre Adélie during winters, we took advantage of the fact that Kerguelen Island is inhabited by these species. The French base Port-aux-Français has a marine laboratory which made it possible to investigate the population of brooders in the coastal waters of the Southern Ocean and their apparent ecological success relative to their developmental pattern.

Results summarized here are mostly taken from the PhD thesis and major articles of the program "Benthos-mac" (Magniez, 1980, 1983; Schatt and Féral, 1991, 1996; Poulin and Féral, 1994, 1995, 1996, 1997, 1998; Poulin *et al*., 2001, 2002) who studied the ecology, life cycle, development and the genetic structuring of the spatangoid sea urchin *Abatus cordatus* (Verrill, 1876) in Kerguelen. Other results were taken from a collaborative project between France and Chile.

Main features of *Abatus cordatus*

The species *A. cordatus* (Fig. 1) lives in the sediment. Females brood eggs and juveniles in four dorsal pouches. The dispersal of this species is therefore characterized by limited mobility among adults and the lack of a free-swimming larval phase. Using scuba and dredging, *A. cordatus* was sampled all around Kerguelen (Fig. 2). The spatial distribution from the island scale to the bay scale shows discontinuities on two levels. First, at the island scale, favorable sectors (principally characterized by jagged coastline with numerous sheltered bays) are separated by linear coastline or swell exposed sectors; secondly, at the bay scale, *A. cordatus* lives in high density, isolated demes in the shallow waters of sheltered bays (inset Fig. 2). Sediment preference ranged from medium to fine sand. The granulometry of the sediment and the lack of predation determine the aggregated spatial distribution pattern. Beside these high density local populations, isolated individuals are found from 1 m to more than 500 m depth.

Isoenzymes analyses (Fig. 3) demonstrated that the geographical distance of differentiation is of the order of 10 km, that the demes are genetically differentiated populations, and that genetic differentiation follows a stepping stone model.

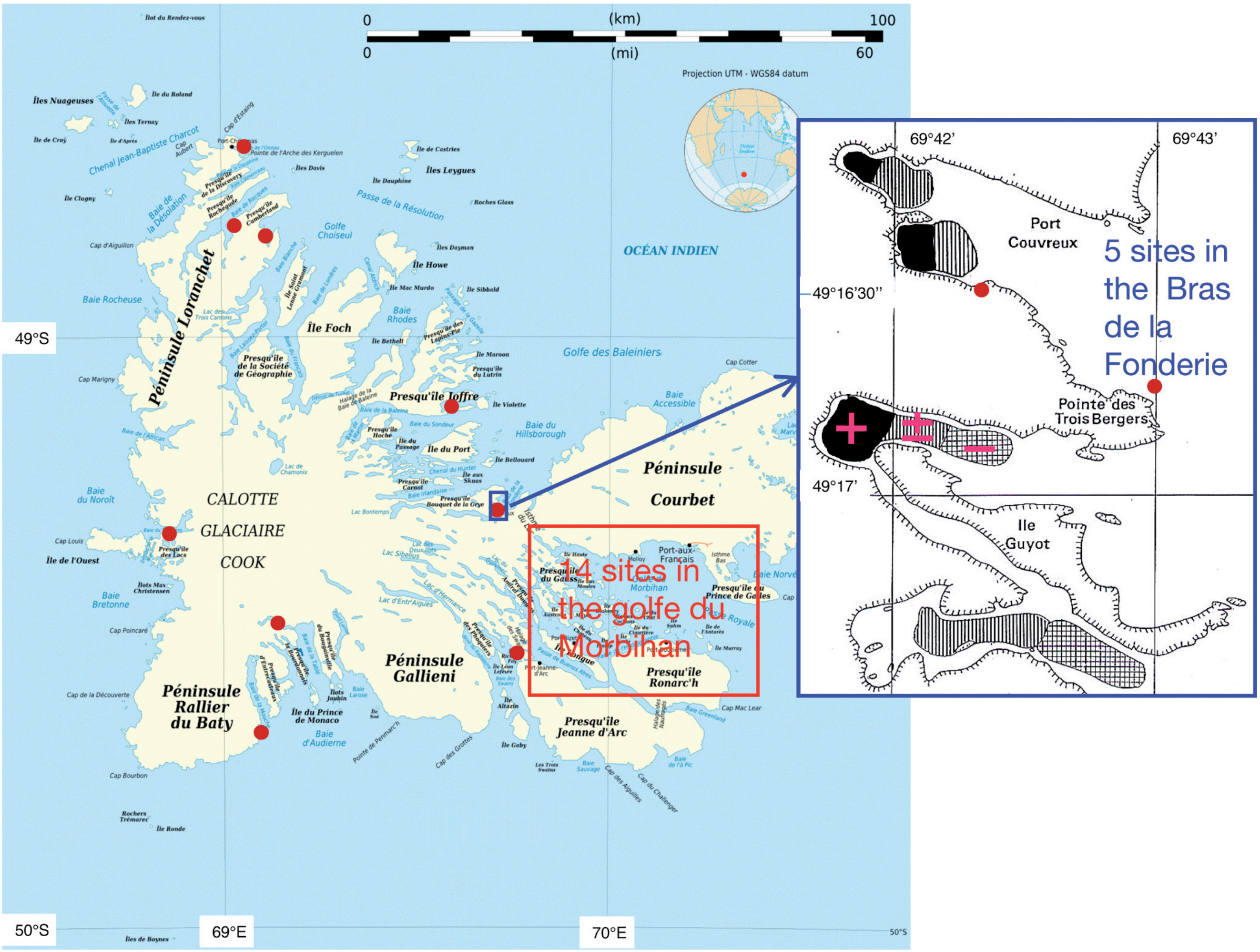

Figure 2. - Sampled sites around Kerguelen (red dots). Inset: details of the distribution pattern of adult *Abatus cordatus* in three very sheltered bays in Bras de la Fonderie [■ high density, ▥ medium density, ▦ low density] showing that *A. cordatus* is characterized by numerous dense isolated demes in shallow waters. The observed densities are decreasing with the depth.

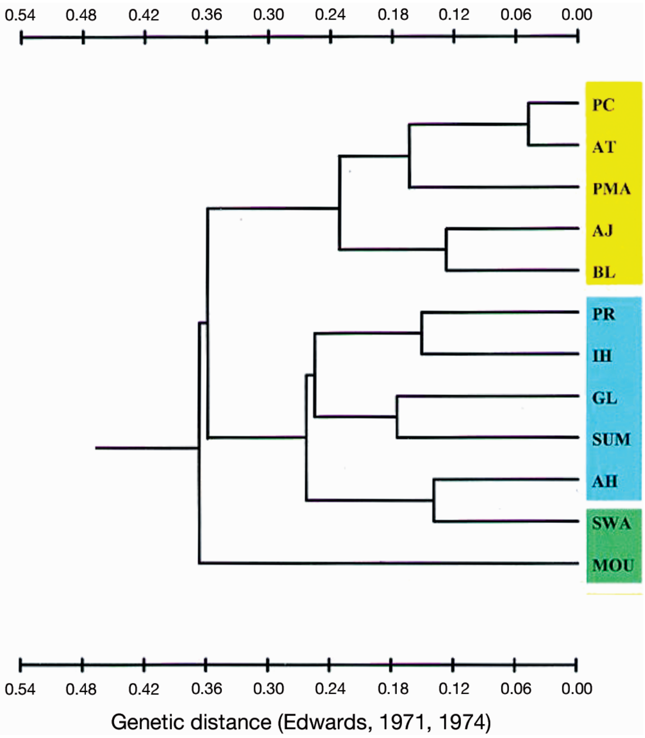

Figure 3. - Edwards's genetic distance among populations of Abatus cordatus sampled along the north (yellow) and the south (green) coasts of Kerguelen and in the Golfe du Morbihan. There is a link between the geographic distance and the importance of the genetic differentiation. North. PC: Port Couvreux, AT: Anse Thomas, PMA: Port Matha, AJ: Anse du Jardin, BL: Baie du Brise Lame; G. Morbihan. PR: Port Raymond, IH: Ile Haute, GL: Îlots Glénan, SUM: Ile Suhm, AH: Anse du Halage; South. SWA: Baie des Swains, MOU: Baie de la Mouche.

Consequences on the long term evolution of the clade

If the likelihood of genetic exchange between populations of species with planktotrophic larvae is high, the reduced gene flow associated with non-dispersive larvae can induce high speciation rates (Fig. 4a). This differential speciation rate model theoretically leads to a progressive increase with time in the proportion of species with non-planktotrophic and non-pelagic development. However, this model alone cannot explain the high diversity of brood protecting echinoids in the Southern Ocean, because it predicts a continuous increase with time in the proportion of such species not only around Antarctica but anywhere else. Indeed, this model does not explain the differences in developmental strategy observed between low and high latitudes.

The climatic evolution of the Antarctic and the Southern Ocean is characterized by a long-term cooling, which started at about 52 Ma, close to the Early/Middle Eocene boundary. This allows the reconsideration of the high speciation rate model (based on isolation by distance) and to reconstruct it with the addition of differential extinction rates between planktotrophic and brooding species in relation to the climatic history of the Antarctic. This differential extinction-rate model between pelagic developing species and brooders could explain the present predominance of brooding echinoids in this area (Fig. 4b). During the coldest phases, the ice sheet blankets the continental shelf, and the surrounding ocean is covered by a thick layer of permanent sea-ice. The direct consequence was a significant reduction in the amount of light, which led to a decrease in primary productivity around Antarctica. The duration of these episodes was typically much larger than the life span of organisms and could have caused the local extinction of many species or even entire clades with planktotrophic development. This model, based on negative selection at the species level, is well supported by Antarctic echinoids. The low number of echinoid families present in Antarctic and Subantarctic areas (6 of 50 known), indicates the extinction of entire planktotrophic taxa and the difficulty for such species to colonize and/or recolonize these areas due to the geographical, bathymetric and hydrological isolation of Antarctica and the barrier posed by the Antarctic circumpolar current.

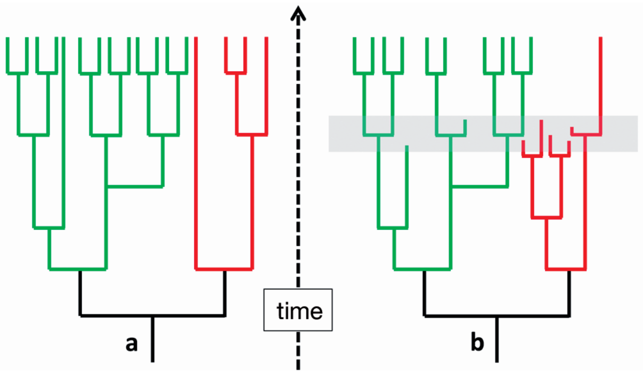

Figure 4. - Hypotheses based on dispersal abilities of species and on their consequences on the long-term evolution of the clade. (a) The high-rate-speciation model: lineage pattern of two clades with different dispersal strategies – differential speciation. (b) The differential extinction-rate model: lineage pattern of clades with different dispersal strategies through a climatic crisis – differential mortalities. Green: low/non dispersal species. Red: high dispersal species. Gray zone symbolizes a climatic crisis.

An increase in the number of brooding species could have also been enhanced through vicariant speciation, particularly during episodes of partial deglaciation. Therefore, the high proportion of brooding species among Antarctic benthic invertebrates could correspond to a macroevolutionary trend resulting from sorting at the species level because of contrasting developmental modes experiencing differential extinction rates during adverse environmental conditions.

A paradoxical observation

In spite of the high number of brooding species, the Antarctic shallow subtidal zone is dominated by numerous individuals of just a few species with a planktotrophic developmental mode, particularly echinoderms. A quick glance into the shallow subtidal zone shows the conspicuousness

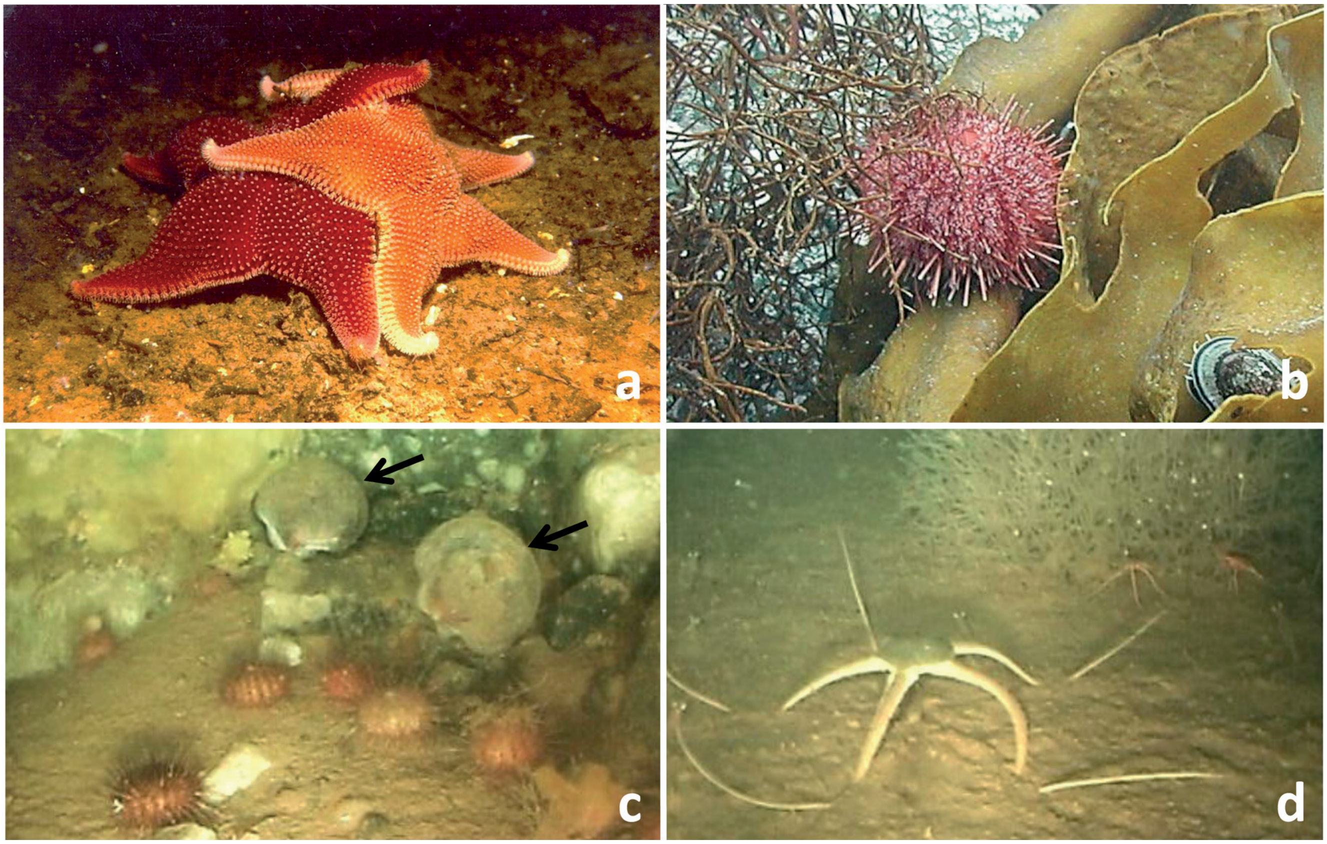

Figure 5. - Examples of Antarctic species with larval phase development (a) *Odontaster validus* (Terre Adélie, Chenal du Lion, 20 m, scuba); (b) *Sterechinus neumayeri* (King George Island, 5 m, scuba); (c) *Adamussium colbecki* (Terre Adélie, Baie de l'Empereur, 58 m, ROV); (d) *Ophionotus victoria* (Terre Adélie, Nunatak du Bon Docteur, 110 m, ROV). © photos by P. Laboute (a) and J.-P. Féral (b to d).

of planktotrophic species, such as the sea urchin *Sterechinus neumayeri* (Meissner, 1900), described as one of the most abundant macrobenthic organisms in shallow Antarctic waters; the asteroids *Odontaster validus* Koehler, 1906, *O. meridionalis* (E.A. Smith, 1876) and *Porania antarctica* E.A. Smith, 1876; the ophiuroid *Ophionotus victoriae* Bell, 1902; the Antarctic scallop *Adamussium colbecki* (Smith, 1902), and the clam *Laternula elliptica* (King and Broderip. 1831). In view of this pattern, and that Antarctica currently experiences interglacial conditions, one might ask if the apparent ecological success of these species is related to the possession of a dispersive larval phase.

Effects of ice disturbances on Antarctic shallow macrobenthos

In shallow Antarctic environments, ice is the most common physical disturbance. There are diverse types of ice-related disturbance such as the formation of icefoot along the coast down to a depth of 10 m, which significantly impacts intertidal and shallow subtidal habitats during most of the year; the formation of anchor ice during winter (down to a depth of 30 m); and the destructive effect of icebergs ploughing down to depths of 500 m. These disturbances favor mobile species and those with pelagic larval development. The occurrence of such disturbances has been recognized as an important factor determining the success of different dispersal strategies. Models have also shown that habitat instability favors species with high dispersal capabilities (such as those with planktotrophic larvae), mainly through recolonization. For marine invertebrates with reduced mobility, larvae are the main vehicles for recolonizing recently disturbed habitats, which typically exist after iceberg scouring events. The Antarctic interglacial environmental condition is characterized by the common occurrence of disturbances and is unlikely to be favorable for brooding species in the shallow subtidal zone. In Subantarctic latitudes, however, where ice impact is less common or nonexistent, ecological dominance of planktotrophic species in shallow habitats is not as evident.

Evolutionary success of brooding versus ecological success of planktotrophy

The arguments presented here suggest that both macro- and microevolutionary processes are responsible for the biodiversity patterns of marine invertebrates currently observed in Antarctica. On the one hand, the high number of brooding invertebrate species (evolutionary success) could be interpreted as the result of a species-sorting process operating during the coolest periods of the late Cenozoic. On the other hand, the current ecological dominance of only a few species with planktotrophic development (ecological success) could be related to the capacity of their larvae to recolonize highly disturbed shallow habitats.

The hypothesis of two processes acting at different timescales, as exemplified here with echinoderms, needs to be broadened to include other taxa. More detailed investigation of the developmental modes of shallow benthic invertebrates and their spatial distribution will enhance our understanding of the evolutionary and ecological processes affecting Antarctic fauna.

Origin and evolution of marine invertebrates in the Southern Ocean

Recent and ongoing studies are using molecular markers to reconstruct the evolutionary history of marine benthos in the Southern Ocean and establish the relationship between Antarctic and Subantarctic areas, as well as shallow and deep-sea water. As shown in our most recent publications on echinoids and limpets, Kerguelen Plateau appears as an indispensable place for such studies, because of its geographic location and the extent of shallow water habitats.

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